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BIOLOGICAL BULLETIN

FORM-REGULATION IN CERIANTHUS, VII.

Tentacle-Reduction and Other Experiments.

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Experiments on Cerianthus Membranaceus.

In the preceding papers certain experiments upon *C. membranaceus* have been mentioned from time to time. It was impossible on account of lack of material to make my studies of this species as full and complete as those of *C. solitarius*. The data obtained were sufficient, however, to show a close correspondence between the two species as regards regulative phenomena.

It was possible to delay tentacle-regeneration by preventing the establishment of internal water-pressure by the methods employed for *C. solitarius*, viz., by reopening at short intervals or by giving the pieces a form such that closure was delayed or prevented.

It is not necessary to give the data of the experiments in full since they add nothing essential to the facts already given for *C. solitarius*. A few points are, however, of some interest especially in view of certain experiments which Loeb performed on this species.

In consequence of the greater thickness and stiffness of the body-wall in this species as compared with *C. solitarius* it is much less difficult to obtain pieces in which the enteron remains more or less widely open for a considerable length of time, in some cases indefinitely. In such pieces tentacle-regeneration is greatly delayed but sooner or later some regeneration does occur.

Loeb ('91, pp. 44 and 45, Figs. 4–6) describes briefly and figures cases of this kind which he obtained by cutting rectangular pieces from one side of the body. His figures show that regeneration of the tentacles occurs but they also show that it is much delayed, since in his Fig. 6, the most advanced stage shown,

the tentacles are only a few millimeters in length, although this piece is two months older than Fig. 4. A piece regenerating in the typical manner during more than two months should possess marginal tentacles 25–40 mm. in length.

Loeb's figures and text indicate that little attention was paid to the internal anatomy of the form. He states that in these rectangular pieces the number of tentacles regenerated was a fraction of the whole number possessed by the original animal corresponding to the fraction of the total circumference represented by the oral end of the rectangular piece, but no reference is made to the correspondence of the tentacles with the intermesenterial chambers. According to Loeb's statements and figures the tentacles appear to arise from the oral cut surface of the piece in each case, but according to my own observations they never arise in this manner. It is difficult to understand how hollow, tubular tentacles could arise directly from the cut edge of the body-wall. This point is of some importance, since if Loeb is correct the influence of internal pressure upon the regeneration of the tentacles becomes at least extremely doubtful.

In the first paper of this series ('03*a*) the typical course of regeneration in *C. solitarius* was described. It was shown there that the new tentacles do not arise at the cut surface but at some little distance from it. The margin of the body-wall rolls inward after section and the tentacles arise at the highest, most oral part of the rounded margin thus formed ('03*a*, Figs. 13–19).

In the specimens of *C. membranaceus* which I have observed the tentacles arise in exactly the same manner. The margin rolls inward and soon changes in the body-wall appear in a region several millimeters distant from the actual cut surface, viz., at the most oral region of the inrolled part. Thus an area extending about the whole circumference is established in which first loss of pigment and reduction in thickness of the body-wall occur, and then the new marginal tentacles appear as minute buds.

In the open pieces corresponding to Loeb's Figs. 4–6 the tentacles arise in exactly the same manner, though much more slowly than in closed pieces. The margin of the piece rolls inward and the new tentacles appear on a part of the body-wall which was originally somewhat aboral to the cut surface.

At first glance it may appear that the regeneration of tentacles in these pieces with open enteron cannot be influenced in any way by internal pressure, but a brief consideration of the matter will be sufficient, I think, to show that even in these pieces some degree of internal pressure is possible. It must be remembered first that the circulatory currents running orally in the intermesenterial chambers continue in pieces with open enteron, except where contraction may bring about the more or less complete obliteration of certain chambers by approximation of the mesenteries. These currents force the water orally into the inrolled region at the oral end. If now the exit of the water from this region be hindered in any way, some slight degree of distention may arise within this rolled portion. Repeated examination of pieces of this kind has led me to the conclusion that the inrolled edge usually presses against the free margins of the mesenteries with some force and may thus hinder in some degree the exit of water. The diagrams 1 and 2 will serve to illustrate this point. In these figures a longitudinal section of the oral end is shown, the cross-hatched portion representing the mesenteries. In Fig. 1 the inrolled edge of the body-wall is shown. Since these pieces represent only a part of the whole circumference of the body the inrolling at the oral end is usually greater than in a complete cylindrical piece, for in the latter the inrolling about the whole circumference soon results in mutual pressure between the various parts of the inrolled portion which prevents further inrolling. The result of the inrolling is to press the cut surface against the margins of the mesenteries. In the collapsed condition these folded and thickened margins form a dense mass and the inrolling of the cut edge upon this must press them still more closely together. In whatever spaces remain between the mesenteries the cilia force the water orally as indicated by the arrows in Figs. 1 and 2. The margins of the mesenteries, being more or less closely pressed together, do not readily permit the escape of the water and consequently a certain degree of pressure may be maintained. Diffusion of water through the walls in this region may also aid in maintaining pressure.

FIG. 1.

FIG. 2.

According to this view these cases are merely special cases of more or less complete local closure of the enteron by inrolling. Various experiments of similar kind have already been described (Child, '04*c*). The only difference between those and these is that here the inrolling is transverse across the oral end and consequently permits the appearance of tentacles upon the whole inrolled portion. Fig. 2 shows the condition of the end after the regeneration of tentacles has begun. By this time the mesenteries in the region of the inrolled margin have acquired new relations to the body-wall such that the margin is held in position. The reduction in thickness of the wall in the upper portion of the inrolled region represents the beginning of tentacle formation. In every case of this kind which I have observed conditions have been similar. The only conclusion possible is that Loeb's statement that the tentacles arise from the cut surface is incorrect and that in the pieces shown in his Figs. 4–6 the tentacles arose in the manner which I have described.

If my explanation is correct, then the results obtained from these open pieces do not contradict the conclusions of my previous papers, viz., that internal water-pressure constitutes a factor in tentacle-regeneration. As regards local pressure due to circulatory currents and its possible effects the statements made in previous papers (Child, '04*b*, '04*c*, '04*d*) will apply here.

In all pieces of this kind the appearance of the tentacles is much delayed and their regeneration is very slow. In no case observed do they ever attain more than a small fraction of the normal length. They are, moreover, always more or less blunt and frequently very irregular, *i. e.*, of different lengths. Similar characteristics were described and discussed for certain cases in *C. solitarius* in a previous paper (Child, 04*c*). Thus in *C. membranaceus* as in *C. solitarius* the facts indicate that internal pressure plays an important rôle in tentacle-regeneration.

The Reduction of Normal Tentacles.

Not only was it possible to retard or inhibit the regeneration of tentacles by reduction of the internal water-pressure, but it was found that fully developed tentacles could be reduced in length by reducing the internal pressure. This process of re-

duction comprises two distinct stages. During the first stage the collapsed tentacles gradually become shorter but do not change in appearance, except to become more and more deeply colored as the pigment-particles are more and more closely approximated with reduction in surface. This reduction continues during a month or more according to various conditions, *e. g.*, the completeness of collapse, the temperature, etc.

If, however, the condition of collapse be continued during a still longer period the tips of the tentacles began to atrophy, becoming darker in color and shrivelled or withered in appearance. This process of atrophy gradually extends proximally along the tentacle if the internal pressure is not reëstablished, until in some cases mere stumps of tentacles remain. The Figs. 3–5 show

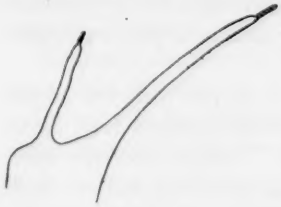

FIG. 3.

FIG. 4.

FIG. 5.

schematically the process of atrophy, one side of the disc with tentacles being shown in section in each figure. Fig. 3 represents a stage in which the marginal tentacles have been reduced by about one half their length and the labial tentacles relatively less. Figs. 4 and 5 represent later stages. In Fig. 5 the long shrivelled distal portion seen in Fig. 4 has been almost completely resorbed. The reduction in size of the disc in consequence of reduced pressure is also indicated in the figures. The difference in appearance between the healthy and shrivelled portions is always marked and visible at a glance. The tips are always much darker in color than the normal tentacle and are irregular in contour, so that the use of the term "shrivelled" is amply justified by their appearance. The proximal healthy portions are about equal in length in all the tentacles of each set, *i. e.*, the atrophy of the tips proceeds with equal rapidity in all tentacles of each set. The tips apparently always remain closed.

A gradual reduction in size of the shriveled portions, due to slow resorption, occurs, and these parts may disappear almost completely, leaving blunt, stump-like tentacles with only slight traces of the dark atrophied tissue at their tips (Fig. 5).

A few experimental data will serve to illustrate more fully this process of atrophy and the conditions under which it occurs.

Series 50.

November 21, 1902. — In three specimens of *C. solitarius* the aboral end was removed by a transverse cut (Fig. 6) and the aboral half of the distal piece was split longitudinally by several irregular cuts in order to render closure impossible or difficult. In these pieces the aboral end was reopened daily or on alternate days in the manner described in a previous paper (Child, '04*b*).

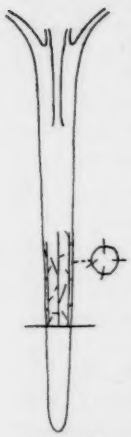

FIG. 6.

Controls were obtained by removing the aboral end from three specimens at the same level as in the experimental pieces. These controls were allowed to remain undisturbed and the cut ends closed in the usual manner. In all specimens, both experimental pieces and controls, the tentacles were measured in a fully distended condition before section. The marginal tentacles were 15–20 mm. in length, differing somewhat in different specimens; the labial tentacles were 5–7 mm.

December 17, 1902. — 26 days after section. Experimental pieces. Reopened daily on alternate days, but sometimes became more or less distended during the intervals, owing to approximation of the cut margins and plugging of the intervening spaces with slime. During this time the tentacles have gradually decreased in length. Marginal tentacles 6–8 mm.; labial tentacles 3 mm.

Controls. The tentacles remained collapsed for a day or two after section, then, as closure of the ends proceeded, the internal water pressure was established and the tentacles became distended. The length of the tentacles is about the same as before section, viz., marginal tentacles 15–20 mm.; labial tentacles 5–7 mm.

From this time on the three experimental pieces were left undisturbed in order to determine whether, after closure of their aboral ends and distension, the tentacles would regain their original length.

December 28. — 37 days after section. Experimental pieces. All healed aborally and fully distended with water. During the eleven days since December 17 the tentacles gradually elongated. In the three pieces the lengths of the tentacles were as follows: marginal tentacles, 12–15 mm., 11–12 mm., 10 mm.; labial tentacles, 5 mm., 4 mm., 3–4 mm.

The longest tentacles at this time belong to the piece which originally possessed the longest tentacles, viz., marginal, 20 mm., labial, 7 mm.

Controls. — In no case do the tentacles show any appreciable reduction in length.

No further increase in length of the tentacles of the experimental pieces occurred.

During the first 26 days the marginal tentacles of the experimental pieces decreased more than 50 per cent. They were more or less completely collapsed during this period, and as a collapsed tentacle is always shorter than one that is distended, it may appear at first glance that the reduction in length represents merely this difference. This, however, is not the case. During the first few days following section the collapsed tentacles were only slightly shorter than they had been when distended and a continuous gradual reduction in length took place up to December 17. During the following period of eleven days in which closure and renewed distension occurred, the tentacles elongated gradually. If the reduction in length had represented only the difference between a collapsed and a distended tentacle it might be expected that the tentacles would regain their original length immediately or almost immediately after the internal pressure and distension were again established. But the increase in length was gradual, although the tentacles were apparently fully distended about December 21. Moreover, they never regained their original length, the maximum being 70 per cent. of the original length.

These facts render it evident that an actual reduction in the

length of the tentacles occurred during the period of reduced water-pressure. The failure of the tentacles to regain their original length is probably due to the loss of vigor observable in all specimens kept without food for a long period and the consequent diminution in internal water-pressure and in the power of growth. Regenerated tentacles never attain the length of the original tentacles and similarly those tentacles elongating after reduction never attain the original length.

In this experiment the process of reduction did not pass beyond the first stage. The tips of the tentacles did not shrivel, but remained healthy and became distended again after closure occurred, though the original length was never attained. It is possible that the frequent partial distension of the tentacles during the intervals between reopening of the aboral end was sufficient to prevent the death of the tissues. As was noted in a previous paper ('04*b*) the pieces must be reopened every few hours in order to prevent partial distension in the intervals, but this is impracticable for the long time necessary for perfect results. Consequently the method is by no means perfect.

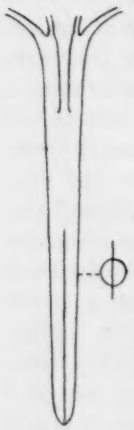

FIG. 7.

Series 19.

September 15, 1903. — In six large specimens the aboral half of the body was split by a longitudinal cut into two parts (Fig. 7).

The object of this experiment was not tentacle reduction but the duplication of the aboral end and consequently the lengths of the tentacles were not determined as frequently during the earlier stages as in experiments on tentacle-reduction. Later, however, when it was observed that these specimens would afford interesting evidence upon this point, measurements of the marginal tentacles were made regularly.

The split aboral portions of these specimens rolled in various ways and closure was greatly delayed, the delay being further increased by the frequent rupture of the delicate new tissue in consequence of contraction during the necessary examinations.

The length of the tentacles in the fully distended specimens before section was as follows: marginal tentacles 25–30 mm.; labial tentacles 12–13 mm.

After section the usual collapse occurred and the tentacles gradually decreased in length.

October 6. — 21 days after section. The pieces have remained almost completely collapsed since section. In some instances a part of the body which was more or less completely closed off became slightly distended, but the frequent examination and removal of slime caused contraction and total collapse. The tentacles were not measured, but marked reduction had occurred during the period of collapse and at this time the tips of all the marginal tentacles were beginning to atrophy.

October 22. — 37 days after section. Two pieces were lost during the interval. The remaining four pieces were somewhat distended with water but any contraction caused loss of water either in consequence of rupture of new tissue or through one or both of the duplicated aboral pores about which the regenerating muscles had not fully developed. Consequently the internal pressure was still relatively very slight. Extensive atrophy of the distal portion of both marginal and labial tentacles had occurred. The marginal tentacles measured 6–7 mm. + 1–2 mm. of shrivelled tissue representing the distal portion of the tentacle. The labial tentacles measured 3–4 mm. + 1 mm. of shrivelled tissue. The basal healthy portions of the tentacles ended bluntly instead of in slender tips as in normal specimens: upon these blunt ends were borne the small shrivelled masses of tissue.

During the following month the pieces succeeded in closing sufficiently to permit considerable increase of internal pressure and no longer lost water during slight contractions.

December 1. — 77 days after section. In three of the pieces the marginal tentacles have increased in length to 10 mm. and the labial tentacles to about 5 mm.

In the fourth specimen the marginal tentacles were 7–8 mm. and the labial tentacles about as before.

In all the atrophied tips have almost completely disappeared, apparently having undergone resorption, but the tentacles are still blunt, not tapering like normal tentacles.

During the next twenty days the pieces showed a considerable reduction in size in consequence of decreasing internal pressure and the distal portions of the tentacles once more began to shrivel.

December 21. — 97 days after section. Marginal tentacles in all four pieces 3–4 mm. + 1–2 mm. of shrivelled tissue.

It was evident at this time that the pieces were becoming exhausted and the experiment was concluded.

In these pieces a gradual reduction in the length of the tentacles occurred during the first two weeks, then the tips began to atrophy, thus reducing the functional portion of the tentacle still further. When closure of the pieces permitted distension the tentacles elongated again and the atrophied tips underwent almost complete resorption. Still later, as the pieces became exhausted and the temperature of the water became lower, the tips of the tentacles once more began to shrivel and at the conclusion of the experiment mere stumps remained.

Reduction of the tentacles was also observed in *C. solitarius* in many œsophageal pieces, *i. e.*, pieces retaining the tentacles and with the aboral end in the œsophageal region (Fig. 8). In such pieces the œsophagus united with the body-wall aborally as in the pieces described in the preceding paper ('04*d*), and except in cases where closure of the body-wall across the end of the œsophagus occured, the internal pressure was never reëstablished.

FIG. 8.

In one piece of this kind which closed aborally across the end of the œsophagus after eleven days the marginal tentacles decreased in length before closure from 25–30 mm. to 10–12 mm. and the labial tentacles from 10–12 mm. to 6–7 mm. After closure the length of the marginal tentacles increased again to about 20 mm. and that of the labial tentacles to about 10 mm. Here the period of collapse was comparatively short and there was no shrivelling of the tips of the tentacles. In another œsophageal piece the marginal tentacles decreased in three months from 35 mm. to mere stumps 3 mm. in length and the labial tentacles from 12 mm. to 1.5 mm. In this case, as in Series 19 above, the reduction of the tentacles consisted at first

merely of a decrease in length, the tissues remaining normal in appearance except as regards the darker color due to the collapsed condition. Later shrivelling of the tips began and continued until only blunt rounded stumps bearing small masses of the dark, shrivelled tissue remained.

In *C. membranaceus* a similar reduction of tentacles was observed, both in pieces which were kept open by artificial means and in œsophageal pieces, but in no case did the distal portions shrivel as in *C. solitarius*. This difference in behavior is probably due to the firmer consistency of the tissues of *C. membranaceus*. In one piece which was opened every day during forty-nine days the marginal tentacles decreased from 40–50 mm. to 10–15 mm. and the labial tentacles from 20 mm. to 3–4 mm. This piece was then allowed to close and become distended and during the next thirty-nine days the marginal tentacles increased in length to 20 mm. and the labial tentacles to 5 mm. In this case the decrease in length was nearly 75 per cent. for the marginal tentacles and about 80 per cent. for the labial tentacles. The marginal tentacles after renewed distension attained nearly 50 per cent. of the original length, the labial tentacles only 25 per cent.

The œsophageal pieces of *C. membranaceus* were not observed to close aborally across the end of the œsophagus in any case. It was therefore impossible to observe increase in length of the tentacles after reduction in these pieces, but marked reduction was observed in all cases. In one piece the marginal tentacles decreased during twenty-seven days from 60 mm. to 20–25 mm. and the labial tentacles from 25 mm. to 10–12 mm. and in others a similar reduction was noted.

It is possible that atrophy of the tips of the tentacles would have occurred if the specimens had been kept for a still longer time. On the other hand this process may be so slow in this species that it is visible merely as a gradual reduction in size.

In view of these facts there can be little doubt that the length of the tentacles is influenced by the internal pressure. The question as to whether it is the general internal pressure which exerts this influence, the effect being merely more conspicuous in the tentacles than elsewhere, or whether local pressure due to currents plays a part must be decided by future experiments.

Various other facts noted in the course of my experiments require mention here. It was noted that regenerating tentacles attained a greater length during the summer months than during winter (*cf.* Child, '03*b*). This difference is probably due, at least in part, to the fact that the internal pressure is higher in summer than in winter in consequence of the greater activity of the cilia in forcing water in through the œsophagus (*cf.* Child, '04*b*). Local pressure must also vary in a similar manner.

It was also observed in a large number of cases that the tentacles of normal animals or regenerated specimens of *C. solitarius* often began to shrivel at the tips in the manner described above when the specimens had been kept in captivity and without special feeding for two months or more. Frequently the marginal tentacles were reduced to a length of 5–6 mm., the specimens appearing otherwise healthy and in good condition, except that the body was in all cases less distended than in newly taken specimens. In the light of the preceding experiments the conclusion is justifiable that the tentacle-reduction in these species is due to decrease in internal water-pressure. The gradual exhaustion of the pieces and the consequent diminution of ciliary activity is without doubt one factor in the result.

As winter approached it was noted that the atrophy of the tentacles began sooner and proceeded farther. During December many of the specimens brought into the laboratory from the bay possessed marginal tentacles only 8–10 mm. in length with atrophied tips and labial tentacles similarly reduced. In nearly all specimens with the tentacles normal in appearance at the time of taking, the atrophy of the tips began within a week or two.

In January and the early part of February, beyond which time my observations do not extend, more than a hundred specimens were taken and of these about 75 per cent. possessed reduced tentacles with atrophied tips when taken. Many of the remainder were specimens with regenerating tentacles, which had undoubtedly been injured.

During the summer and autumn reduced tentacles with atrophied tips were not found on any specimen at the time of taking. Moreover, the tentacles of summer and autumn specimens were

always much longer than those of winter specimens even when the latter were not atrophied.

These facts leave no room for doubt that the reduction of the tentacles and the loss of their tips is a normal phenomenon during the winter months. I was able, however, to bring about this change experimentally in September and October, *i. e.*, at a time when newly taken specimens showed no trace of such a change.

Unfortunately it was impossible to continue observations during the spring. I have no doubt, however, that as the temperature of the water rose the internal pressure became greater and the tentacles increased in length again.

The animals do not thrive in aquaria with standing water and it was not practicable to supply the aquaria with running water kept at a constant temperature approaching that of the water in summer. For these reasons the experiment of keeping the animals with reduced tentacles in water of a higher temperature than that in which they had been living could not be carried out satisfactorily. I venture to predict, however, that the result of such an experiment would be an elongation of the reduced tentacles, though probably they would never attain the full summer length unless the animals were well fed.

There is no ground for supposing that the specimens with atrophied tentacles were in a pathological condition. Specimens which were in this condition when taken lived for months in captivity and regenerated as completely as other specimens. After atrophy of a certain portion of a tentacle the atrophied portion was gradually absorbed and the remaining proximal portion retained a perfectly healthy appearance until the gradual decrease in internal pressure due to exhaustion brought about a further atrophy. These reduced tentacles could be distinguished at once from normal tentacles by their blunt tips.

The only conclusion possible in view of the facts appears to me to be that any condition which reduces the internal water-pressure to a sufficient extent will bring about the atrophy of the tentacles. Experimentally reduction of pressure was accomplished by preventing closure, but it is clear that any condition which decreases ciliary activity will decrease the internal pres-

sure, since the force of the inward current through the œsophagus is reduced. The force of circulatory currents in the body must be similary reduced and consequently any local pressure due to them is also reduced.

Decrease in temperature is a condition which reduces ciliary activity. It follows that in winter specimens the cilia must be much less active than in summer specimens. Winter specimens are visibly less distended than summer specimens. I can see no escape from the conclusion that the atrophy of the tentacles in winter specimens is due as in experimental pieces to a long-continued reduction to a relatively low level of the internal water-pressure, resulting in this case from the reduction of ciliary activity in consequence of low temperature.

The fact that the shrivelling of the tentacle always begins at the tip and proceeds gradually in the proximal direction is of some importance. If this process is the result of decrease in the general internal pressure why should the reduction proceed from the tip? According to the laws of hydrostatics the internal pressure must be the same in all parts of the enteric cavity, consequently when reduction of the pressure occurs it occurs at all points. This being the case why should a slight reduction of pressure affect merely the tip of the tentacle, while a greater reduction causes atrophy of a larger part?

In the present state of our knowledge two explanations of this fact appear possible. It may be that the distal portions of the tentacle exist under relatively unfavorable conditions of nutrition as compared with the proximal portions. The small size of the tentacular cavity in this region and the consequent imperfect circulation of fluid and also its distance from the central cavity where most of the digestion probably occurs, afford a possible basis for such an assumption. If the stimulus of internal pressure is effective upon the tissues of *Cerianthus* we should expect to find the poorly nourished parts of the body more sensitive than other portions to decrease in this stimulus. According to this view reduction of internal pressure might result in atrophy beginning at the tips of the tentacles and proceeding proximally according to the degree and duration of the reduction.

The second explanation is based upon the possible effect of local pressure due to circulatory currents. It is evident that with approach toward the distal end of the tentacle the circulatory currents must decrease in force and volume since in the confined space of the tentacular cavity the friction between the currents in opposite directions is relatively greater than in the enteron. The force and volume of the currents must also depend upon the degree of distension of the tentacle and body and therefore upon the general internal pressure. If, therefore, the internal pressure be reduced, the tentacular cavity decreases in size, and the circulatory currents are practically eliminated in the extreme distal portion of the tentacles: local pressure at the tip of the tentacle is thus reduced. It is possible that this is a factor in bringing about a condition of malnutrition. According to this view the atrophy of the distal portion may be the result of the reduction of local pressure in the distal portion of the tentacle in consequence of the reduction in force and volume of the circulatory current. The larger, proximal portion is still of sufficient size even under reduced pressure to permit the existence of these currents.

Since I have mentioned in previous papers certain facts which seem to indicate the possibility that local pressure due to circulatory currents may constitute a formative factor in *Cerianthus* the possible effect of these currents is mentioned in this connection. It is possible that both reduction in local pressure and malnutrition of the distal portions of the tentacles may coöperate in causing atrophy under reduced general pressure. But whatever interpretation may be placed upon the facts, the occurrence of atrophy under reduced internal pressure is clearly shown.

Summary.

1. Pieces of *C. membranaceus* in which the enteron remains widely open to the exterior may show some degree of tentacle-regeneration. In such pieces the inrolling of the oral margin and the pressure of the cut surface against the mesenteries may be sufficient to prevent the escape of water and thus permit the establishment of some degree of internal pressure within the in-

rolled portion. In all cases of this kind tentacle-regeneration is much delayed and never proceeds far.

2. It is possible by reduction of the internal water-pressure to cause reduction of fully grown normal tentacles in both *C. solitarius* and *C. membranaceus*. The first stage in the reduction consists in a gradual decrease in length and size of the tentacles: in *C. membranaceus* no further change was observed, but in *C. solitarius* shrivelling and atrophy of the tentacles began at the tips if the reduced pressure continued. In specimens which were kept widely open the tentacles were reduced to mere stumps a few millimeters in length.

3. If specimens with partially atrophied tentacles be allowed to close, the basal healthy portion of the tentacle begins to extend as the internal pressure is reëstablished.

4. Atrophy of the distal portion of the tentacles occurs in specimens of *C. solitarius* which are kept for a long time without food and is also found in nearly all specimens taken during the midwinter season.

5. Since the internal pressure in normal animals is due primarily to the activity of cilia any conditions which reduce the activity of the cilia reduce the pressure. Low temperature and starvation or exhaustion cause reduction in ciliary activity and so in internal pressure. If these conditions continue for a certain length of time atrophy begins at the tips of the tentacles, proceeding proximally as the reduction in pressure continues.

6. The fact that atrophy due to reduced pressure always begins at the tip of the tentacle may be explained by the relatively greater reduction in the force and volume of the circulatory currents in the distal region in consequence of the smaller size of the tentacular cavity in that region or it may be due to a condition of malnutrition in the distal regions of the tentacles which in turn is the result of the small size of the tentacular cavity and the distance from the main digestive cavity. In this condition the distal regions of the tentacle are less capable of continuing their existence under unfavorable conditions (*e. g.*, reduced pressure) than the more proximal portions. Possibly both of these factors are concerned in the result.

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UNIVERSITY OF CHICAGO, November, 1903.

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LOCOMOTION IN BATRACHOSEPS WITH SEVERED NERVE-CORD.

CHARLES D. SNYDER.

The earlier discoveries in the anatomy and physiology of the nervous system led to the conception that the nervous mechanisms of the human body were under the control of a single center, the brain.[1] Discoveries, which have been made in the field of comparative physiology during the past fifty years, however, are lead- to a very different conception.

Not only the spinal cord,[2] but also the brain,[3] is being regarded not as a single nerve-center but as a segmental series of many nerve-centers. Furthermore the idea is gaining ground that true nerve-centers are probably not so greatly differentiated one from the other, — that their respective protoplasmic contents are not so different in nature, as was once supposed. On the other hand it is pointed out that specific differences in the nervous substance is to be looked for in the sense-organs, in the peripheral nerve-substance, rather than in the central organs. Accordingly the central nervous system is to be regarded primarily as a special conduction substance by means of which the sense organs are able to communicate with the various physiological structures in which the efferent nerve-fibers find their termination.[4]

The observations reported in the present paper furnish additional evidence in support of this segmental theory of the central nervous system. In order to make the viewpoint of interpretation of results clearer the work of two other authors will be first briefly reviewed.

Friedländer[5] observed that coördination of the longitudinal

[1] Schiff, "Lehrbuch der Physiologie," 1858, s. 194. Foster, "History of Physiology," 1901, p. 257 ff. Steiner, "Die Functionen des Centralnervensystems und ihre Phylogenese," 2te Abtheilung, Die Fische, 1888, s. 35.

[2] Sherrington in Schaefer's "Text-book of Physiology," p. 816. Loeb, *Arch. f. d. ges. Physiologie*, Bd. 96, s. 536, 1903.

[3] Grünbaum and Sherrington, *Proc. of Roy. Soc.*, Vol. 69, 1901.

[4] Loeb, "Comparative Physiology of the Brain and Comparative Psychology," 1901.

[5] Friedländer, B., "Physiologie des Centralnervensystem," *Arch. f. ges. Physiologie*, Bd. 58, s. 168, 1894.

muscles in earthworms was not disturbed by removal of a small piece of the nerve-cord, that the circular muscles failed to contract only in the region where the cord was removed and that elsewhere they continued to contract rythmically. If the posterior part of such a worm lay on a smooth surface it would allow itself to be dragged along by the part anterior to the section. If, however, the posterior part be dragged over a rough surface, moistened blotting paper for instance, its segments would begin active, rythmical contractions and coöperate with the anterior part in progressive locomotion.

That one part of the body in these worms was not dependent on the nerve-cord of the other part was still better shown in a worm which was cut cross-wise into two halves. The halves were fastened together again by a string. The anterior half, pulling on the posterior half, especially when the latter lay on a rough surface, would produce coördinated movements in the posterior half.

In another experiment only the posterior half was used. It was placed on papers of two grades of roughness, the anterior part on the rougher, the posterior part on the smoother paper. A pull on the rougher paper started up locomotor contractions in the foremost segments; the other segments remained inactive while being dragged over the smooth paper, notwithstanding the fact that the cord was intact in the entire piece of the animal which was under observation.

These phenomena in worms with severed nerve-cords were explained as follows: One segment, shortening, produces a pull on the next segment in the body and thereby stretches the skin of that segment. This stretching process sets up sensory impulses which, passing into their segmental ganglion, are reflected back as motor impulses to muscles of the same segment. The muscle contraction so produced in turn exerts a pull on the skin of the next segment and thereby gives rise to another cycle of sensory-motor impulses, which, as mere nerve-impulses, do not necessarily pass beyond the boundaries of the segment where they originated. And so on, from segment to segment, a motor impulse started at *a* may be transmitted to segments *b*, *c*, *d*, etc., without any impulses whatsoever passing over the fibers in the

nerve-cord which directly connect the ganglia. In short, coördinated locomotion is secured without the nerve cord, as such, coming into play at all. In their passage the nervous impulses involved, according to this conception, do not follow a straight path with side-paths at each segment, but rather follow a path which may best be described as a line of loops.

Friedländer concluded that locomotor movements in the earthworm should not be regarded as the result of a single impulse (say of the anterior segment) which passes through the length of the body, but rather should it be regarded as the result of impulses given off by each segment separately.

2. That coördinated movements in animals higher than worms may be set up and maintained, with the spinal cord brought into use only in spots, as it were, rather than as an entire and single organ, has been recently demonstrated in a remarkable way by the experiments of Phillipson.[1]

It has been known for some time[2] that, if a dog with a sectioned cord be supported so that its hind legs hang freely in space, the legs spontaneously begin an alternate flexor-extensor movement.

Phillipson obtained this so-called pendulum movement of the legs in a dog with sectioned nerve-cord. The movement lasted sometimes for more than an hour; it could be accelerated into a veritable gallop by gently pulling the tail of the animal. The valuable part of this experimenter's work, however, lies in the complete analysis which he was able to make of the various steps involved in the process of locomotion. From his experiments and observations on this dog with the severed nerve-cord, he drew conclusions concerning locomotion in the hind legs of normal dogs somewhat as follows:

The hind-foot of a dog during extension gently comes in contact with the ground; this foot-contact produces a feeble excitation which brings on a flexing of the metatarsals with the sole of the foot supported against the ground. The resistance of the ground against this flexing of the metatarsals produces a sensory-motor wave which brings a sudden halt to all muscular

[1] Phillipson, Maurice, *Comptes Rendus*, Vol. 136, p. 61, 1903.

[2] Freusberg, *Archiv f. die ges. Physiologie*, "Reflex Bewegung beim Hunde.," 1874, Bd. IX., s. 358.

action which in turn throws the body forward. The shock produced by the sudden halt of muscular action causes flexion of the limb which has just reached the limit of extension, and the pulling of the skin at the inguinal region by this same extension, starts up extensor movements in the opposite limb, which in its turn coming in contact with the ground goes through the same cycle of movements just completed in its fellow. And so on, the action of one leg determines that of the other, so that not only walking but running movements in the hind-legs may be, and probably are, kept up indefinitely, involving the use of no more of the nerve-cord than that part in which these simple sensory-motor impulses may be exchanged.

According to Phillipson's analysis it appears quite possible that, *after progressive locomotion has once been started in a normal dog, it might walk or even run a distance without any additional impulses passing down from the upper region of the spinal cord.*

3. The question now arises, *could normal walking movements in the hind legs of an animal be initiated without any impulses whatsoever, for the purpose, coming into the lumbar centers from levels of the cord higher, say, than the mid-dorsal region, or from levels higher than the lumbar region itself.*

Loeb[1] has already suggested that the pendulum movements in the hind-legs of a dog with severed nerve-cord may be caused by the stretching of the skin on the sides of the body produced by holding up the front part of the animal. He further held the opinion that if the beast could stand at all on its legs it probably could go through the coördinate movements necessary for walking. For, if the fore-legs took forward steps that action would produce a pull on the sides of the body, stretching the skin. This stretching would create sensory stimuli that would pass into the lumbar region of the cord whence extensor motor stimuli would pass into one leg or the other and thus start up the cycle of ambulatory motions described by Phillipson. This view of the possibility of coördinating anterior and posterior locomotion in a vertebrate with severed nerve-cord receives strong support from the experiments and observations of Friedländer. But it may be

[1] Loeb, Jacques, "Beiträge zur Gehirnphysiologie der Würmer." *Arch. f. d. ges. Physiologie*, 1894, 56, s. 268.

objected that results obtained from an animal of such pronounced metameric structure as that of the earthworm cannot be applied in the case of vertebrates; that if "the nerve-cord of the earthworm is an apparatus by means of which reflexes may be transferred from one segment to the other"[1] it does not follow that the nerve-cord of a vertebrate in its activity can be reduced to elements equally simple.

In uninjured land animals of the bilateral types progressive locomotion is usually initiated by forward or lateral movements of the anterior part of the body. This action produces an effect on the passive posterior part of the body, especially in the skin, where sensory stimuli may be set up. These sensory stimuli may be aroused in two ways. First, by tugging, the skin is subjected to stretching stimuli; second, by dragging even the slightest distance, the ventral surface of the body, and therefore of the skin of creeping animals, is subjected to a series of rapid, successive impacts against the inequalities of the ground-surface. In other words, by dragging *the skin is subjected to friction stimuli in addition to stretching stimuli.*

Now since the skin is always subjected to more or less such treatment in the initiation of locomotor movements, it is reasonable to suppose that a characteristic combination of sensory stimuli is thereby produced which may be able to set up motor stimuli in centers of corresponding levels. One may suppose moreover that these motor stimuli do not result in vague, purposeless reflexes, but rather that they result in definite, unvarying coördinations; that they are operative and effective without intervening stimuli from other regions of the nerve-cord.

In other words, *a definite combination of sensory stimuli in one region, occasioned by a definite motor activity in another region, may be a sufficient signal for locomotor activity in the region receiving such sensory stimuli.*

4. At the suggestion of Dr. Loeb, for whose constant assistance and kindly interest in my work I wish here to express my best thanks, I began some experiments during February of this year to test the truth of the ideas set forth in the foregoing paragraphs.

[1] Freidländer, *loc. cit.*, p. 206.

The animal selected for experimentation was *Batrachoseps*. This is a small batrachian with a long, slender body and ridiculously short, slender legs which, while perfectly functional, are not depended upon to carry on all the work of locomotion. The complete musculature of the body-walls and of the long, slender tail is evidence that they, too, at times assist mightily in locomotion. Indeed in the normal animal one sees that for leisurely movements only the legs are used, the body, always moist and somewhat slimy, being dragged passively along; and that for locomotion under pressure of unusual excitement the powerful body and tail muscles are brought into play. The body throughout its length is well marked off externally into segments, or metameres. One could not find an animal that combines the locomotor structures of both annelid and vertebrate better than does *Batrachoseps*.

There are twenty distinct segments between the girdles of these animals. Of the twenty-two specimens operated upon, the cord was severed between the fifth and sixth segments of some; between the tenth and eleventh of others; and of still others, between the fifteenth and sixteenth segments. In a few cases the section was made nearer the girdles, which always resulted in paralysis of the legs.

They usually recovered from the effects of the chloroform-ether mixture within five to fifteen minutes after taking it. The operation which consisted of simply snipping the spinal column in two with strong fine-pointed scissors, or destroying the nerve-cord by probing with a needle point, took only a minute or a minute and a half. Care was taken to injure as few of the muscles of the body-wall as possible and to avoid puncturing the peritoneum and the large blood-vessels, excepting in those cases where the animals were cut entirely in two.

In two specimens a piece of the spinal column about two mm. in length was removed. Shock effects occurred in only a few cases, which will be spoken of later on.

In all cases where the operation itself was successful and where the cord was not severed too near one or the other of the girdles coördinated movements were observed, not only between the members of the fore-legs and of the hind-legs, but also between the pairs themselves.

The animals operated upon were kept in broad flat-bottomed dishes. The floors of the dishes were kept covered with moistened layers of filter paper. During resting periods the animals were protected from the light of the room by being covered with fresh leaves or moist filter paper, and by covering over the dishes with towels.

When these coverings were removed the animals, usually asleep at the time, would sooner or later become aware that they were out in the open. They would then become restless. In their efforts to get under cover again one could note very easily the manner of their progress. Movements were usually initiated by the anterior parts turning to the one side and then to the other several times and finally back to the tail, often moving across it and twisting the body into a loop. During these movements the posterior parts would lie motionless and apparently helpless. After a number of these attempts at progressive locomotion the animal would start out straight ahead. The hind parts being unresponsive, it would tug and pull with the fore-legs in an effort to drag the helpless part along, and, in spite of the great length of the body and tail, and the extreme delicateness of the legs, the animal often succeeding in doing this.

The results of this tugging and dragging of the hind parts, while always the same, may be obtained by various methods, and were observed in my experiments as follows:

(*a*) Sometimes when the animals struck out in a forward direction and began to tug at the hind parts the hind-legs would begin to assist *before they were dragged in the least.* Their movements while slower than the fore-legs *coöperated toward forward locomotion*, and, furthermore, *were flexed and extended alternately*, that is, *they took forward steps alternately.*

(*b*) At other times no movements occurred in the hind-legs until the hind parts had been dragged along for a distance. The legs would then begin coördinate movements as described above. Sometimes the legs happened to be extended back along the sides of the tail and held up (surface tension of water and mucus alone being sufficient to support the weight of the legs) so that the toes did not touch the ground-surfaces. In such cases it was noticed that the hind-legs remained irresponsive for a longer time

than if they had been pendent enough so that the toes also touched and dragged along the ground.

(*c*) Coöperation on the part of the hind-legs could be started by touching with a pencil-point the skin of the sides of the body posterior to the section in the cord, or by touching the toes or the heels.

(*d*) A number of specimens would walk perfectly normally on their hind-legs when the front part of the body was held up and carried forward slowly. The walking movements would begin sometimes at once without dragging, sometimes after the hind-legs were dragged for a distance.

Experiments were made cutting *Batrachoseps* entirely in two as Friedländer had done with earthworms. The section was made at various levels between the girdles. Nothing but simple reflexes were obtained from the posterior halves although the pieces lived for days. The anterior halves, however, seemed to suffer no depression whatever. As soon as they recovered from the effects of the anæsthetic, they moved about in a manner that, with the exception of the awkwardness produced by the absence of the customary weight and resistance of the postetior parts and of the exhaltation produced by the operation, was perfectly normal. One of these anterior pieces lived for twenty-four hours. An hour before it died it was still breathing and moving about normally.

These results are about what one would expect to find in *Batrachoseps*. For, unlike earthworms, they cannot depend alone on the skin for respiration or upon an uncertain circulation. After sectioning the body the posterior half is deprived entirely of the benefits of the pharyngeal breathing and of the heart-beat, which continue on in the anterior half uninterrupted. After cutting an earthworm in two, respiration and the circulation can go on in the posterior half as well as they do in the anterior half. Hence the nervous responses in the one half are not different from what they are in the other half.[1]

5. *Summary and Conclusions.* — The results of the foregoing experiments on *Batrachoseps* may be summed up, and conclusions may be drawn, as follows :

[1] Friedländer, *loc. cit.*, p. 190.

(*a*) The coördinating center of locomotion in the hind-legs is located between the sixteenth and the eighteenth segments of the trunk.

(*b*) Walking movements in the hind legs after the spinal-cord is severed are due primarily not to impulses arising in the spinal centers, but to impulses that arise in the sensory cells of the periphery.

(*c*) These sensory impulses may be produced in the skin and muscles of the body-walls by stretching-stimuli; in the skin of the body-walls and of the legs by mechanical-impact-stimuli (friction- or tapping-stimuli).

(*d*) The fact that *Batrachoseps* with sectioned cords walk on their hind-legs when carried along by their fore-legs supports Loeb's idea that the same thing would obtain in dogs with sectioned cords if they could only stand up, or if their legs were shorter so that they might be effective in their movements when the trunk is prostrate. The difficulty in the dog is not due to the absence of the walking apparatus, but to the absence of "tone" in the muscles.

(*e*) Perhaps the essential thing supplied by the nerve-cord, as such, to the limbs during locomotion is this tone, this complimentary resistance of the muscles toward each other which keeps them ready for instantaneous regulated action, and which is probably maintained by impulses passing down from the organs or centers of equilibrium.

(*f*) If respiration could be properly maintained in the posterior half of *Batrachoseps* after being severed entirely from the anterior half, it is probable that walking movements could be started in the hind-legs by stretching-, or friction-, or tapping-stimuli, that is, by tugging gently at the front end of the posterior half, or by dragging it a distance over moist blotting paper, or by fastening it by means of a string to the anterior half and allowing the latter (which can walk along spontaneously) to pull at, or drag, the former along.

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BUTLER'S GARTER SNAKE.

ALEXANDER G. RUTHVEN.

[From the University Museum, University of Michigan.]

The garter snake, *Eutænia butleri* Cope, has been the subject of considerable discussion among herpetologists in spite of the fact that only five specimens were known. In 1888, Professor Cope ('89, p. 399) first recognized and described the species on the basis of a single specimen (Purdue Univ. Catalogue, No. 264) sent to him by Mr. A. W. Butler. This specimen was thought to have come from Richmond, Indiana, but it was unlabeled when Mr. Butler received it from Purdue University, so it may or may not have come from there. In 1895, Mr. Reddick ('96, p. 261) took another specimen (Univ. of Ind. Cat. No. 110) at the Indiana University Biological Station at Turkey Lake, Kosciusko County, Indiana. There are two specimens in the museum of the Academy of Natural Sciences of Philadelphia (Cat. No. 6523) labeled by Professor Cope, which are described by Mr. A. E. Brown ('01, p. 27) and credited by him to southeastern Indiana. But in a letter April 15, 1904, he says concerning these specimens, "The locality given is Miami river, which probably means Ohio." The fifth specimen recorded (U. S. N. M. Cat. No. 21692) was collected by Mr. Philip Kirsch at Waterloo, Indiana, and is described by Dr. Stejneger ('94, pp. 593–594).

Professor Cope examined the type and on the basis of its distinctive characters considered it a good species, a view supported by Dr. Stejneger after a study of the specimen from Waterloo, Indiana. Mr. Brown, however, upon a study of the two specimens in the collection of the Philadelphia Academy of Natural Sciences, and for the reason that there were so few specimens known, considered them anomalies of *E. sirtalis sirtalis*, with considerable reason, for it seems as if four specimens (the specimen from Turkey Lake is described for the first time in this paper) is entirely too small a number upon which to form a species. Particularly is this true in a genus like *Eutænia*, in which

the individual variation is so great. It was, therefore, with considerable interest that I found last winter, while working over the collection of reptiles in the University Museum at the University of Michigan, a number of specimens of this rare snake. I have been able to make a study of the character of these specimens, and to supplement this by a study of the coloration and, to a certain extent, of the habits of a number of living specimens which have been collected about Ann Arbor. The present paper embodies the results of this investigation, and the data on all the other specimens recorded.

Through the courtesy of Dr. W. J. Moenkhaus, the specimen taken at Turkey Lake, Ind., has been examined, and Dr. Stejneger has very kindly sent me a detailed description of the specimen from Waterloo, Ind. I am indebted to Mr. A. E. Brown for a description of the specimens in the Museum of the Academy of Natural Sciences of Philadelphia, who also examined two specimens from Ann Arbor, Mich., and pronounced them the same form as those in his possession. I wish also at this time to acknowledge my indebtedness to Mr. Chas. C. Adams, Curator of the University Museum, University of Michigan, for assistance in the prosecution of this work and in the publication of the results.

I have been unable to examine the type, which according to Professor Cope is Cat. No. 264 at Purdue University. The specimen sent to me as the type is Cat. No. 81, and while labeled *E. butleri*, is not that form, but a normal specimen of *E. sirtalis sirtalis*, and corresponds in no way to Professor Cope's description of the type. I have also, through the kindness of Professor S. Coulter, examined the garter snakes in the Butler collection at Purdue University, but found no specimens of *butleri* among them.

It is important to diagnose this form, as it is very probable that many specimens are at present stored in museums under other names or undetermined. In this connection, one calls to mind a paper by Dr. H. L. Clark of Olivet College, Olivet, Michigan, on the occurrence of the short mouthed snake in Michigan ('03, pp. 83–88). Last year Dr. Clark found six specimens of a snake, which upon the authority of Mr. S. Garmen and Dr. Stejneger,

he called *E. brachystoma* Cope. I have, through the courtesy of Dr. Clark, examined three of these specimens and we both agree that they are the same form as those which I identified as *E. butleri.* The only specimen of *E. brachystoma* ever recorded is in the collection of the Philadelphia Academy of Natural Sciences and Mr. Brown says of this specimen that, "There is little ground for thinking it other than a dwarfed *E. sirtalis sirtalis*" ('01, p. 28). After a comparison with specimens of *E. butleri* from here, Mr. Brown writes me as follows, "I have reëxamined the type of *E. brachystoma* Cope, and still find no reason to believe it other than an anomalous *E. sirtalis sirtalis.* Cope says 'it is small but not young,' I myself see no way to determine this, it may or may not be so. The specimen was about ready to shed when he got it, which of course obscured the pattern. I cannot think it is the same as *E. butleri.*"

Dr. Stejneger suggested ('94, p. 594) that the specimen collected near Chicago in 1874, by Mr. E. W. Nelson, and labeled by Davis and Rice *E. vagrans* ('83, p. 30), might prove to be another specimen of *butleri*, but through the courtesy of Dr. U. S. Grant, Curator of the Museum at Northwestern University, I have been able to examine this specimen, and it is undoubtedly an *E. vagrans.* It differs from *butleri* most noticeably in having the dorsal scales in 21 rows, 8 supralabials on the right side and 9 on the left, and in the larger number of urosteges and gastrosteges, which are respectively 86 and 170.

Habits.

Very little has been recorded on the habits of this snake. Its movements as Mr. Reddick describes them, are extremely awkward. It seems compelled to exert much effort in crawling, and its efforts to escape capture are often ludicrous. In captivity it takes readily to water, and is an exceedingly graceful swimmer. Its awkwardness in crawling, contrasted with its ease of motion in water, together with the fact that all the specimens recorded have been taken near water, bears out the statement of Dr. Clark ('03, p. 87) that "Although not aquatic this species likes water and is found only in its immediate vicinity." It is one of the first Michigan snakes to come out in the spring; a

single specimen having been taken as early as March 18, which is the earliest date recorded for any snake from this locality. The latest date at which a specimen has been taken is September 22, but the time of hibernation is undoubtedly much later than this. It is an exceedingly amiable little snake, and no amount of rough handling will induce it to strike, which is in marked contrast to the pugnacity of *E. sirtalis sirtalis*, when captured. As far as I have been able to observe, its diet in captivity consists chiefly of earthworms and small frogs. Its breeding habits are unknown; in one specimen (U. of M. Mus. Cat., No. 31612) taken May 28, 1904, at Sandusky, Ohio, there are 8 eggs in each oviduct about 20 mm. long and 12 mm. broad. In another specimen (U. of M. Mus. Cat., No. 31624) taken June 3, 1904, at Ann Arbor, Michigan, there are 7 eggs in the right and 5 in the left oviduct. These eggs are about 12 mm. long and 10 mm. broad.

Distribution.

The geographical range of *butleri*, as we know it, is very limited. As will be seen from the table, it occurs in the northern and, if the locality of the type is correct, the southeastern parts of Indiana, in the north and southwestern parts of Ohio and in southern Michigan. It apparently cannot be abundant in Indiana or more specimens would have been taken, as many reptiles have been collected there and the state has been worked by Dr. O. P. Hay, who describes ('92, p. 528) the type as being the only specimen known at that time. In southern Michigan, however, it occurs quite commonly, at least near Ann Arbor. Of its occurrence in other parts of Michigan, nothing can be said, except of the six specimens taken by Dr. Clark at Olivet.

Diagnosis.

Body stout, tapering abruptly at both ends. Head conical, smaller than neck, muzzle a little protuberant. Tail short. Dorsal scales in 19 rows, all carinated, the first much the largest. Supralabials 6–6, the fifth the largest, the third and fourth, entering the orbit. Infralabials 8–8. Preoculars 1–1. Postoculars 3–3. Temporals 1–1, the second large, extending from labials to parietals. Gastrosteges 140. Urosteges 61. Length

230 mm. Tail 60 mm. Color above olive brown, with two alternate rows of black spots above the lateral stripe, and one below; the dorsal spots forming a broken border to the dorsal stripe. Color below light olivaceous, sparsely speckled with black, with a row of gastrostegeal spots on either side. The dorsal stripe occupies the median and the two half rows of scales on either side; anteriorly bright yellow, it extends well up between the parietals; posteriorly it fades out quickly to a greenish yellow, and loses its distinctness on the tail. Color below the lateral stripe the same as above, olive brown. Lateral stripes anteriorly bright sulphur yellow, broad, occupying all of the third, the upper half of the second and the lower half of the fourth rows of dorsal scales on the anterior half of the body. On the posterior half they occupy exclusively the second and third rows to the vent; but they never descend below the middle of the second row; at the vent they widen out to cover part of the first, all of the second and third, and all of the fourth rows; posteriorly to the vent, olive in color, occupying but one row of scales, the first, and becoming more and more indistinct toward the end of the tail.

FIG. 1. Eutænia butleri Cope. Ann Arbor, Washtenaw Co., Michigan, Cat. No. 30460, U. of M. Museum.

Anteriorly the lateral stripe expands to form a large yellow patch on either side of the neck, in which occur two black spots one on the right side, and one on the left. These spots are continuations of the row below the lateral stripe. There is also a black spot, just above the sixth supralabial, that is prolonged in front to the lower edge of the upper postocular. Above the black line formed by the continuation of this spot, the head is uniformly brownish olive, with the exception of a black patch on the parietals in which are located the prominent bright yellow parietal spots. The supralabials are dusky yellow, narrowly margined with black; the yellow extending up to the black line, thus including the two lower postoculars, and part of the first temporal. In front of the eye, the yellow of the supralabials extends onto the preocular, where it gradually fades into the olive-brown of the top of the head. The eye is surrounded by a nar-

row ring of black; as is also the nostril. There is also a black line between the preocular and loreal. Chin white. Throat yellowish.

The specimen upon which I have based the above description as being typical of the form, since I have been unable to examine the type, is a specimen taken on the bank of the Huron river, near Ann Arbor, Michigan, by myself, September 22, 1903 (U. of M. Mus. Cat. No. 30642). It is not a mature specimen, and for this reason the color pattern is more distinct than in older specimens, for the ground color tends to become darker and to obscure the spots in adults. This is the only difference except in size to be observed between old and young specimens.

Variation.

Contrary to the usual tendency among the species of *Eutænia*, the specimens of *butleri*, which I have examined, show but little individual variation from the type as described by Cope, or the specimen which I have chosen as being most nearly normal. It is an interesting coincidence, that all the specimens previously recorded (Phila. Acad. of Sci. Cat. No. 6523, U. S. N. M. Cat. No. 21692, and Purdue Univ. Cat. No. (type) 264), possess 7 supralabials on either side, while in the specimens which I have examined these are nearly always 6–6, but occasionally 6–7 and in three cases 7–7; when there are 6 supralabials, the fifth is always the largest; when there are 7, the extra one is apparently formed by a divison of the fifth, as may be seen in two cases (U. of M. Mus. Cat. No. 30683 and 30506), in which the fifth is only partially divided. The supralabials are nearly always 8–8; in two cases (U. of M. Mus. Cat. No. 30471–30407*a*) they are 9–9, and in one case the extra one is on one side only. The oculars are normally 1–3, with an occasional variation to 1–2. Concerning the disputed second temporal, there is in most cases a single large temporal in the second row, as is given by Prof. Cope for the type. When there are two, the upper is always very much the smaller, and generally so much so as to be surrounded by the lower on the lower and posterior sides. In specimen No. 6523b Phila. Acad. of Sciences, the lower one of the second row seems to have divided length-

wise so as to form a long narrow scale which is in contact with the first temporal. The gastrosteges vary in number in 20 specimens from 131–154 with an average of 139; the urosteges in 19 specimens from 50–71 with an average of 60. The coloration is remarkably constant, the only differences observed being the presence of lighter ground color in the young which causes the lateral spots to stand out more prominently than in the older specimens, where the color varies to a brownish black, which may quite obscure the spots.

For convenience, the data on the specimens previously described and on fifteen specimens which I have examined have been tabulated on following pages. It will be seen from this table that there is, as was shown above, some individual variation, yet the distinctive characters are so pronounced and constant, that in the case of none of the thirty specimens examined was I in doubt as to where to place a single individual.

Affinities of Butleri.

Professor Cope's statement, that *E. butleri* "is remarkably distinct from anything which occurs in the United States" is born out by the specimens now at hand. As was mentioned above, the range of variation is never great enough to make the determination of a specimen doubtful. They resemble in this region the *E. sirtalis* group more closely than any other, and it was for this reason that Mr. Brown considered his specimens aberrant forms of *sirtalis sirtalis*. The finding of so many specimens, however, makes this view untenable, and the question then arises, whether it is to be considered as a variety of *E. sirtalis*, or as a distinct species.

The number of gastrosteges, and superior and inferior labials are normally less than in any *E. sirtalis* except *E. s. leptocephala*. The gastrosteges in one instance are 154, a common number in *sirtalis sirtalis*, and the supralabials are sometimes seven, the normal number for *sirtalis sirtalis* which also occasionally has nine infralabials, as occurs in two specimens of *butleri*. It might seem from this, as Mr. Brown has suggested to me, that *butleri* bears the same relation to *E. s. sirtalis* as *E. s. leptocephala* does. He regards *E. s. leptocephala* as a degenerate form of *E. s. sirtalis*,

Specimens.	Locality and Date.	Supra-labials.	Infra-labials.	Oculars.	Tem porals.	Uro-steges.	Gastro-steges	Total Length.	Length of Tail	Collector.
1. Purdue Univ., Cat. No. 264. (Type.)	Richmond, Wayne Co., Indiana. (?)	7	8	1–3	1–1	62	144			
2. U. S. N. M., Cat. No. 21692.	Waterloo, Steuben Co., Indiana, July 17, 1893.	R 7 L 7	R 8 L 9	R 1–3 L 1–2	R 1–2 L 1–2	57	131	530mm	115mm	Philip Kirsch.
3. Univ. of Ind., Cat. No. 110.	Turkey Lake, Kosciusko Co., Indiana.	R 6 L 7	R 8 L 8	R 1–3 L 1–3	R 1–2 L 1–1	60	134			G. Reddick.
4. Philadelphia Acad. of Nat. Sci., Cat. No. 6523*a*.	Miami River, Ohio. (?)	R 7 L 7	R 8 L 8	R 1–3 L 1–3	R 1–2 L 1–2	71	144	475mm	107mm	
5. Philadelphia Acad. of Nat. Sci., Cat. No. 6523*b*.	Miami River, Ohio. (?)	R 7 L 7	R 8 L 8	R 1–3 L 1–3	R 1–2 L 1–2	68	142	440mm	112mm	
6. Univ. of Mich., Cat. No. 30642.	Ann Arbor, Washtenaw Co, Mich., Sept. 22, 1903.	R 6 L 6	R 8 L 8	R 1–3 L 1–3	R 1–1 L 1–1	61	140	230mm	60mm	Riley & Ruthven.
7. Univ. of Mich., Cat. No. 30641.	Ann Arbor, Washtenaw Co., Mich., Sept. 22, 1903.	R 6 L 6	R 8 L 8	R 1–3 L 1–3	R 1–1 L 1–1	57	136	220mm	50mm	Riley & Ruthven.
8. Univ. of Mich., Cat. No. 30863.	Chelsea, Washtenaw Co., Mich., Oct. 28, 1903.	R 7 L 7	R 8 L 8	R 1–3 L 1–3	? ?	62	138	240mm	55mm	E. N. Transeau.
9. Univ. of Mich., Cat. No. 30460.	Ann Arbor, Washtenaw Co., Mich., April 28, 1903.	R 6 L 6	R 8 L 8	R 1–2 L 1–3	R 1–1 L 1–1	50	154	415mm	90mm	N. A. Wood.
10. Univ. of Mich., Cat. No. 30506.	Chelsea, Washtenaw Co., Mich., May 10, 1903.	R 6 L 6	R 8 L 8	R 1–3 L 1–3	R 1–2 L 1–2	58	135	450mm	110mm	Chas. C. Adams.
11. Univ. of Mich., Cat. No. 30109.	Ann Arbor, Washtenaw Co., Mich., March 18, 1903.	R 6 L 6	R 8 L 8	R 1–2 L 1–2	R 1–1 L 1–1	54	140	480mm	105mm	N. A. Wood.
12. Univ. of Mich., Cat. No. 30471.	Ann Arbor, Washtenaw Co., Mich., May 2, 1903.	R 6 L 6	R 9 L 9	R 1–3 L 1–3	R 1–1 L 1–2	55	140	415mm	90mm	Chas. C. Adams.
13. Univ. of Mich., Cat. No. 30407*a*.	Ann Arbor, Washtenaw Co., Mich., April 7, 1900.	R 6 L 6	R 9 L 9	R 1–3 L 1–3	R 1–1 L 1–1	Tail broken	137			Ida M. Hopson.

Specimens.	Locality and Date.	Supra-labials.	Infra-labials.	Oculars.	Tem-porals.	Uro-steges.	Gastro-steges.	Total Length.	Length of Tail.	Collector.
14. Univ. of Mich., Cat. No. 30407*b*.	Ann Arbor, Washtenaw Co., Mich., April 7, 1900.	R 6 L 6	R 8 L 8	R 1-3 L 1-3	R 1-2 L 1-2	67	139	406mm	106mm	Ida M. Hopson.
15. Univ. of Mich., Cat. No. 31383.	Ann Arbor, Washtenaw Co., Mich., April 27, 1901.	R 6 L 7	R 8 L 8	R 1-2 L 1-2	R 1-1 L 1-2	61	141			Florence J. Hagle.
16. Univ. of Mich , Cat. No. 31613.	Sandusky, Erie Co., Ohio, May 28, 1904.	R 7 L 6	R 8 L 8	R 1-3 L 1-3	R 1-2 L 1-2	62	138	445mm	105mm	E. L. Moseley.
17. Univ. of Mich., Cat. No. 31614.	Sandusky, Erie Co., Ohio, May 28, 1904.	R 6 L 6	R 8 L 8	R 1-3 L 1-3	R 1-2 L 1-2	60	136	465mm	112mm	E. L. Moseley.
18. Univ. of Mich., Cat. No. 31612.	Sandusky, Erie Co., Ohio, May 28, 1904.	R 7 L 7	R 8 L 8	R 1-3 L 1-3	R 1-1 L 1-1	60	139			E. L. Moseley.
19. Univ. of Mich., Cat. No. 31627.	Brighton, Livingston Co., Mich., April 23, 1904.	R 7 L 6	R 8 L 8	R 1-3 L 1-3	R 1-2 L 1-2	63	146			B. K. Burgess.
20. Univ. of Mich., Cat. No. 31628.	Brighton, Livingston Co., Mich., April 23, 1904.	R 7 L 7	R 8 L 8	R 1-3 L 1-4	R 1-2 L 1-2	55	139			B. K. Burgess.

a view which is also held by Professor Cope ('92, p. 660) and Dr. Stejneger ('93, p. 214). This view is perhaps supported by the great variability of *leptocephala*, but *leptocephala* occurs in a distinct region while *butleri* occurs in the same region, in the same habitat and in almost equal abundance with typical forms of *E. s. sirtalis;* and at the same time its distinctive characters are so constant, that no variations have been found that can be regarded as transitional forms between the two species. The average number of gastrosteges in *butleri* is about 139 while in *sirtalis sirtalis* it is about 151. The temporals are also more constant than appears in the table; it is true that there is not always a single large temporal in the second row, but when there are two as in *sirtalis sirtalis*, the upper one, as far as we know is always much smaller than the lower one, which lies posterior and inferior to it. The form and coloration are, however, the most characteristic features. The body is more robust, the tail shorter, and the head smaller and more conical than in *sirtalis sirtalis*. As stated under variation, the color is remarkably constant for a member of this genus and while there is much color variation in the *E. sirtalis* group, I have never seen a variation that could be confused with *butleri*. Its striking coloration, robust form, small indistinct head and peculiar movements, make this snake very conspicuous and renders it almost impossible to confuse it with any other form. I have not seen enough specimens to determine its relationships with other groups, but the coloration, position of the lateral stripe, and reduced number of infralabials point strongly toward *E. radix* which meets it on the west.

Desirable as it is, therefore, to cut down the species in this genus, it must, I think, be concluded, from the specimens which have been collected that *Eutænia butleri* is a good species.

SYNONYMY.

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1892. *Eutænia butlerii*, Cope, Proc. U. S. Nat. Mus., XIV., p. 651.

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TENACITY OF LIFE IN ANTS.

ADELE M. FIELDE.

Maimed Ants.

Remarkable tenacity of life is sometimes exhibited by ants lacking a portion of the body.

A queen, *Stenamma fulvum piceum*, deprived of the funicles of her antennæ, lived fourteen months in one of my artificial nests, where she laid eggs, sought her own food, and received kindly treatment from the resident workers and several unmutilated queens.

The head of a *Formica fusca subsericea* worker under my observation, continued to move its antennæ seven hours after decapitation.

Ants lacking a leg or two may live several weeks. A *Stenamma fulvum* worker, deprived of its mesothoracic pair of legs, was returned by me to an artificial nest where were hundreds of its former comrades and it safely lived there a month or more, disproving any general assertion that ants destroy maimed members of their colony.

Worker ants deprived of the abdomen sometimes run with great speed, continue to care for the young in the nest, fight with aliens of their own or other species, and they may for some days behave as if unconscious of loss. A *Stenamma fulvum* queen deprived of her abdomen lived thereafter for fourteen days in one of my artificial nests, and was seen to eat. A *Formica subsericea* worker lived without her abdomen for five days.

M. Charles Janet mentions[1] an ant that lived nineteen days after decapitation. In experiments made by me, headless ants have continued to walk about for many days. In all these experiments aseptic surgery was attempted, the instruments used being carefully sterilized. The Petri cells in which the maimed ants were

[1] "*Extrait des Compte rèndus hebdomadaires des Séance de l' Acadèmie des Sciences*," Paris, 11 juillet, 1898, p. 130.

kept were frequently cleansed with 80 per cent. alcohol, and only distilled water was used in wetting the enclosed sponges. Care was taken to maintain hygienic conditions at all times during the life of the ant. In these experiments a *Stenamma fulvum* worker lived ten days without her head. A *Formica subsericea* worker lived fifteen days without her head. Of seven decapitated *Camponotus pennsylvanicus* workers, three lived five days; two lived twenty-one days; one lived thirty days; and one lived forty-one days. The last two mentioned were the largest, being thirteen millimeters long. After decapitation, they were kept for four days at a temperature of about 10° C. or 50° F. and afterward in the natural summer temperature of the laboratory.[1] The ant that lived forty-one days after decapitation walked about in the cell until two days before her death, and during the last two days gave evidence of life by a twitching of the legs when I touched her.

Submergence.

While making experiments in June, 1904, with a view to ascertaining how long ants could live under water,[2] I came to suspect that the death of ants submerged less than seventy-two hours was caused by bacteria rather than by deprivation of oxygen. Later in the summer I therefore made further experiments, merging the ants in distilled water, and keeping them in the dark at a temperature of about 10° C. or 50° F. Under these conditions the ants survived much longer periods of submergence.

Of eighteen *Stenamma fulvum* submerged four days, seventeen revived and twelve fully recovered.

Of fourteen *Stenamma fulvum* submerged six days, six revived, and one fully recovered.

Of twelve *Stenamma fulvum* submerged eight days in sixty-five cubic centimeters of water, seven revived and fully recovered.

Of seven *Camponotus pennsylvanicus* submerged eight days, four revived, fully recovered, and were returned to their old associates.

[1] Nearly all the experiments recorded in this paper were made at the Marine Biological Laboratory at Woods Holl, Mass., during the summer and autumn of 1904.

[2] "Observations on Ants in their Relation to Temperature and to Submergence," A. M. Fielde, Biological Bulletin, Vol. VII., No. 3, August, 1904, p. 170.

The ants recovering after submergence were those of large stature among their kind.

Dwarf Ants.

The ability of the larva to successfully enter the pupal-stage of development at any time after about half its normal size has been attained, helps to assure the persistence of a harried community. Under propitious conditions the larva grows to the size of an adult ant, expels the contents of the alimentary canal, and eats nothing during the five or ten days preceding pupation. But if suddenly deprived of food it may enter the resting stage when half-grown and may ultimately become a perfectly formed dwarf. I sequestered many fat, healthy, half-grown larvæ of *Stenamma fulvum*, put them in the care of fewer nurses than could regurgitate food to all of them, and supplied but little nutriment to the segregated group. Many of the larvæ soon entered the resting stage and later on became dwarf workers, only three or four millimeters in length, while the length of workers of their species is usually from five or seven millimeters. A corresponding diminution in the stature of a man would take from one to two feet from his height. The dwarf workers were wholly normal in their faculties and activities, and were markedly assiduous in their care of the young. On the other hand, larvæ poorly fed may miserably linger, as if waiting for better times. In one case under my observation, an ill fed larva remained such for one hundred and forty days, although constantly in summer temperature, and it then died without pupating.

Deprivation of Food.

Although ants manifestly suffer and soon die if deprived of water, they can exist for many days without food. In the following tests the ants were kept in Petri cells, ten centimeters in diameter, and not more than five ants were enclosed in any one cell. All the cells were kept in darkness or very dim light. At intervals, never exceeding four days, the cells and the enclosed sponges were cleansed with 80 per cent. alcohol, to prevent microscopic growths which might furnish nourishment to the ants. The cells contained only the ants used in the experiment, and a

bit of sponge saturated with distilled water. Care was taken to ensure good ventilation and all other conditions were made hygienic, that there might be no cause of death other than that of deprivation of food. The starving ants did not manifestly weaken after long abstinence but collapsed suddenly and finally, giving no premonitory evidences of exhaustion.

Of thirty *Cremastogaster lineolata*, segregated on July 2, 1904, ten lived so long as ten days and only one lived so long as eighteen days without food.

Of thirteen *Camponotus herculeanus pictus* workers, two lived seven days; two, fourteen days; one, eighteen days; one, twenty-three days; two, twenty-four days; one, twenty-six days; and one, twenty-nine days. On the tenth day of fasting, I found three of these ants killed and dismembered, with an appearance of having been chewed. In all the cells, this was the only group where the ants attacked their companions in tribulation. As ants sometimes quarrel with their mates when food is plentiful, this affray cannot be fairly attributed to a cannibalistic tendency in this species.

Of nine *Stenamma fulvum* workers, two lived eighteen days; one, twenty-seven days; one, twenty-nine days; one, thirty-two days; two, thirty-six days; one, thirty-eight days; and one, forty-six days. The last to die measured seven millimeters.

Of eight *Camponotus pennsylvanicus* workers, one lived fourteen days; two, eighteen days; one, twenty-one days; one, twenty-two days; one, thirty-nine days; one, forty-five days, and one, forty-seven days. The last two mentioned were fourteen millimeters long, and were larger than any of those that died earlier.

Of five *Formica lasiodes* workers, one lived ten days; two, eighteen days; one, thirty-nine days. An isolated queen of this species, lived from July 2 to August 31, just sixty days. During her isolation, she deposited seven eggs, the seventh being laid on the twenty-first day of her fasting. Any egg discovered in the cell was at once removed.

Of nine *Formica fusca subsericea* workers, picked up from a roadside and segregated without feeding on July 3, one lived ten days; one, seventy-one days; and the other seven were all alive on October 18. Possibly the remarkable capability of these ants

to live without food, enhances their value in slavery, where other species so often hold them.

Of two *Camponotus castaneus americanus* workers,[1] measuring thirteen millimeters, one lived fifty-four days, and the other lived more than a hundred days.

Two winged queens of *Camponotus americanus*, eighteen millimeters in length, and at least three months old, were established in a separate cell on July 13. One of them dropped her wings on July 31, while the other continued to wear her wings. No eggs were laid by either and both were alive on October 18.

Elimination of Inedible Substances.

The skill with which ants eliminate from their food supply such inedible substances as may be commingled therewith, was shown in the action of *Stenamma fulvum piceum* toward certain dye-stuffs that I mixed with their nutriment. Into each of four similar Fielde nests, C, I, T, and M, I put one queen and fifty workers, with a few half-grown larvæ. During three months no food was given to these ants other than what is hereinafter mentioned. The dye-stuffs were first triturated, molasses was added to make with them a thick paste, and a portion of the paste was then placed in the food-room of the nest. For the C nest, cochineal was commingled with the molasses; for the I nest, indigo; and for the T nest, tumeric; while for the M nest, molasses alone was provided. During the three months hardly any ants died in either nest. There was no evidence that any larva was devoured; and as the introduced larvæ appeared in due time in active life, they must have been nourished solely upon regurgitated food. In only one of the nests were any eggs seen, their absence probably being due to deprivation of insect food.

In all of the nests the finely pulverized inedible substances mixed with the molasses were separated in the mouths of the ants from the nutrient fluid, and were cast out in minute pellets, forming a characteristically colored heap in a corner of each nest, C, I, and T. In the M nest, a smaller pile of brown pellets indicated that non-nutritious particles had been rejected from the unmixed molasses.

[1] These ants were kindly identified for me by Dr. W. M. Wheeler.

Such preclusion of innutrient matter from the alimentary canal must greatly conserve the physical energy of the ants in the processes of digestion.

Avoidance of Poisons.

Ants that had fasted ten days did not partake of sweets in which poisons were incorporated, although their equally hungry mates ate the unpoisoned sweets with avidity.

When the ants were compelled to walk over a mixture of one gram of corrosive sublimate with two cubic centimeters of molasses, they afterward cleaned their feet with tongue and mandibles, and then evinced much distress in cleaning their mouths, but nearly all of them survived the experience.

When one gram of potassium cyanide was dissolved in five cubic centimeters of molasses, and the ants compelled to walk upon the solution, they appeared to die within a few seconds after touching the feet with the tongue, but they all revived some minutes or hours later and continued their normal activities.

When one gram of carbolic acid crystals was dissolved in two cubic centimeters of molasses, the ants compelled to walk upon the solution cleaned their feet with their tongues and mandibles, evinced much distress, and died after some hours or days, with no subsequent resuscitation.

In the experiments with poisons, the ants employed were *Cremastogoster lineolata*, *Stenamma fulvum*, *Lasius latipes*, *Formica subsericea*, *Camponotus pennsylvanicus* and *Camponotus castaneus americanus*. In these experiments the largest ants were latest in succumbing to the effects of the administered poisons. *Camponotus americanus*, about thirteen millimeters in length, lived several days after the administration of the carbolic acid, and in a natural environment might possibly have remedied their ills.

Regurgitation of Food.

Whether the regurgitation of food be a simple reflex or an altruistic act, it was practiced by some of the ants when there was little to confer upon a starving comrade. One *Camponotus pennsylvanicus* worker was seen to make unsuccessful effort to regurgitate food to another on the thirty-first, and also on the thirty-sixth day of fasting.

FIG. 2. *Camponotus castaneus americanus*, slightly magnified, showing five workers engaged in the regurgitation of food to their comrades, and four winged queens. From a photograph by Mr. J. G. Hubbard and Dr. O. S. Strong.

A winged queen of *Camponotus americanus* regurgitated food to her deälated sister queen, on the twenty-fifth, the thirty-fifth, the fortieth and the sixty-second day of fasting, the visible transfer of food occupying several minutes.

The ants cannot, however, be considered to virtually possess a common stomach. There was great difference in the periods within which ants of the same colony and species, in the same cell, perished from deprivation of food.

The feeding of the larva by different ant-nurses doubtless conduces to its vigor, because the nurses forage in diverse localities bringing back nutriment containing unlike chemical elements which they transfer by regurgitation to the growing young.

Doubtless the adult ants also benefit greatly through the habit of regurgitating food to each other. Going afield in many directions, one finds nectar, another berries, another nut-kernels, another insect flesh, another egg-yolk, and many give of their garnered nutriment to their companions in the nest. Variety in the food supply for each individual is in fairly direct ratio to the number of fellow-workers who reach new sources of sustenance. Vigor gained by the adults through varied diet and the assimilation of new chemical compositions, would tend to increase the stamina of the growing young through an improved pabulum as well as through heredity.

There is notable difference in the average size and vigor of the individuals in different colonies of ants of the same species.

Relation of Sex and Food to Tenacity of Life.

Male ants shared all tests here presented, but whatever the test undergone, the males showed far less tenacity of life than did either the queens or the workers.

If, as has long been held, the product of unfertilized ant-eggs are males while the product of fertilized ant-eggs are females, then it may be that the absence of certain chemical elements contained in the fertilized egg is a cause of lesser tenacity of life in the male ants.

In all tests of vitality, ants of largest stature among their species showed greatest tenacity of life. Whether the test applied

were endurance of heat,[1] submergence in water, deprivation of food, excision of parts of the body, or administration of poison, the larger the ant, the more probable its survival.

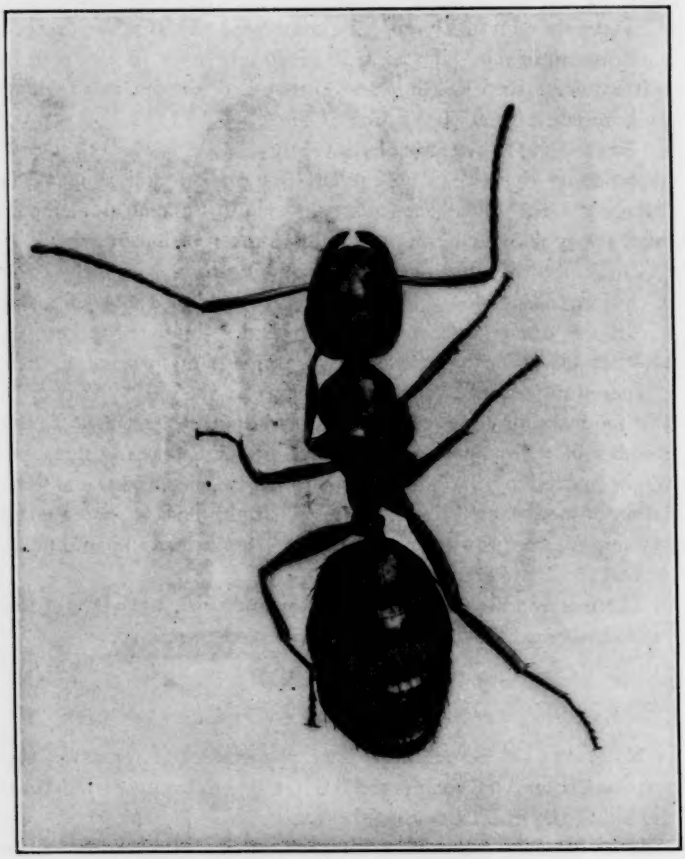

FIG. 1. *Camponotus pennsylvanicus* worker. × 6. From a photograph taken by Mr. J. G. Hubbard and Dr. O. S. Strong, and retouched by Dr. J. H. Macgregor.

There appears to be also a relation between size and natural longevity. Two hundred *Stenamma fulvum piceum* workers,

[1] See paper referred to in previous note, BIOLOGICAL BULLETIN, June, 1904.

majors, minors and minims, were segregated by me in August, 1901, and were kept under observation until August, 1904. At the end of the three years there were eleven survivors, and ten of these were of the largest stature attained by these ants, seven millimeters. Queens, whose longevity probably exceeds that of workers, are ordinarily of larger stature than they.

It has long been known that the size of an ant depends on the quantity and quality of nutriment taken while in the larval stage; but larval nutrition determines not only the size of the ant within the limits of its species; it also determines something of greater influence in the life of the individual and the persistence of the tribe, the probabilities of survival under adverse conditions.

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